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glows ere it passed beyond the Pacific, new charms were added to the place. We saw the beautiful crested valley quails fly on whirring wing from the mesas and the chaparral to the dense foliage of the live oak, where their leader called to the night's repose; we heard the long-continued ringing note of the ground tit (*Chamæa fasciata*) from the thicket by the road-side; we heard—almost *felt*—the dismal, multitudinous barkings and howlings of a coyote that watched us from a ridge not far away, and could hardly believe one poor beast could carry on such a concert; we saw and heard and felt a hundred beauties which delight the soul and fill it with happy memories. We enjoyed most the fish we didn't catch.

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THE PHYLOGENY OF THE CAMELIDÆ.

BY E. D. COPE.

AS is well known, the camels form a well-distinguished division of the Artiodactyla, or even-toed ungulates. The prominent features which separate them, osteologically speaking, from other Artiodactyla are three, viz., the absence of a canal of the cervical vertebræ which in other Mammalia encloses the vertebral artery (Fig. 1); the presence of an incisor tooth on each side of the

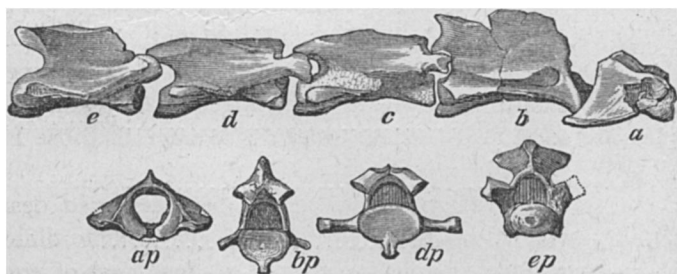


FIG. 1.—*Poebrotherium labiatum* Cope; five anterior cervical vertebræ, showing absence of vertebral arterial canal; one-half natural size. Figs. *p*, posterior views of vertebræ lettered to correspond with those represented above them. Original, from specimen from White River bed of Colorado, represented in Fig. 7.

upper jaw (Fig. 12); and thirdly, the incompleteness of the keels of the distal ends of the metapodial bones (Fig. 2). This character and that of the presence of incisors, are primitive conditions common to all the early Mammalia. The peculiar cervical vertebræ constitute a specialization, but whether degenerative or pro-

gressive remains to be ascertained. In one respect this line exhibits a high specialization, which is present at the earliest known period of its history. This consists in the reduction of the lateral (II and V) metapodial bones, so that but two functional toes remain (see Fig. 1, *c-f*). This condition has been reached by the more typical artiodactyles after a much longer lapse of time, for most of the extinct and recent types display lateral digits in a well-developed or rudimentary condition; in but few of them have they totally disappeared. In another respect the line of the camels attains a higher specialization than that of the typical ruminants, although its beginning is that which is common to the entire suborder. This is in the dentition. The reduction in numbers of teeth showed by Owen to characterize the historical succession of all Mammalia, is carried further in the molar series of camels than in any hoofed order; for in the final term or genus, *Eschatus* (Cope), there is but one premolar left in the upper jaw, and that is reduced to a simple cone. The true molars never reach the complexity of those of the other line, of the Bovidæ or oxen, nor do they become prismatic as in that family, but retain the short crown well distinguished from long roots, which belongs to all the earlier Mammalia.

The successional reduction in the numbers of premolar teeth in the family of the Camelidæ is shown in the following table.¹ There is seen in the genera *Protauchenia* and *Palauchenia* a tendency to an increase of complication of the fourth inferior premolar.

I. Premolar teeth $\frac{4}{2}$.	
P-m. 1 separated by diastema.....	<i>Procamelus</i> Leidy.
II. Premolar teeth $\frac{4}{3}$.	
P-m. II below wanting.....	<i>Palauchenia</i> Cope.
III. Premolar teeth $\frac{4}{3}$.	
Fourth inferior premolar triangular.....	<i>Camelus</i> Linn.
Fourth inferior premolar composed of two crescents, which enclose a lake (an inferior P-m. 3?).....	<i>Palauchenia</i> Owen.
Fourth inferior premolar composed of two crescents, with two posterior tubercles behind them.....	<i>Protauchenia</i> Branco.
IV. Premolar teeth $\frac{4}{2}$.	
Fourth premolar below triangular.....	<i>Auchenia</i> Illiger.
V. Premolar teeth $\frac{4}{1}$.	
Fourth superior premolar composed of two crescents.....	<i>Holomeniscus</i> Cope.
Fourth superior premolar consisting of a simple cone.....	<i>Eschatus</i> Cope.

¹From Proceedings Amer. Philosoph. Soc. 1884, p. 16.

The only genera which include existing species are *Camelus* and *Auchenia*, the camels and llamas respectively. It may be remarked that the latter genus, which is confined to the new world, is more specialized than *Camelus*, which is restricted to the old world.

Ancestral to the Camelidæ is the genus *Protolabis* Cope (Fig. 10), which agrees with *Procamelus* (Fig. 11), the earliest genus of that family in most respects, but differs decidedly in having a full set of superior incisor teeth. In this genus we reach the stage, in tracing back the ancestry of the camels, which we find represented by *Oreodon* in the series of the Chevrotains (Tragulidæ), or the *Gelocus* in the line of the cattle and deer. It is probable, though not certain, that in *Protolabis* the metapodial bones are combined into a cannon bone as in the Camelidæ. If so it differs materially from its predecessor, the genus *Poebrotherium*, and must be regarded as the type of a special family, the *Protolabididæ*.

The *Poebrotheriidæ* have their general characters like those of the *Protolabididæ*, but the metapodial bones are entirely distinct (Figs. 3, 7). The molar teeth are truly selenodont, and the crescents, as in the other families, are but four in number. The premolars are entirely different in form from the molars, and the last one in the upper jaw consists of but two crescents, as in ruminants generally.

The family which should be ancestral to the *Poebrotheriidæ* is not certainly known. It should possess the foot-characters of the latter with quadritubercular inferior and superior molars. That is,

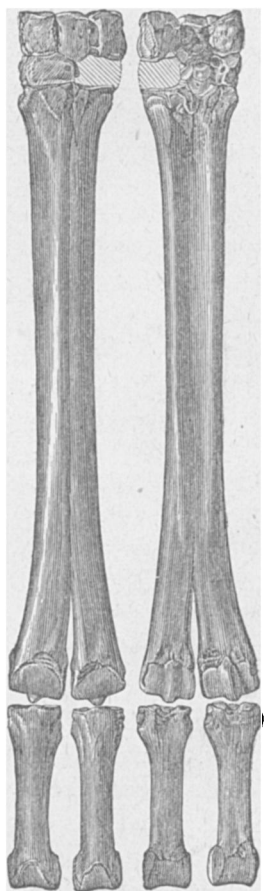


FIG. 2. — Carpus, cannon bone and first phalanges of *Procamelus occidentalis* Leidy, from New Mexico, from individual Fig. 12; *a*, anterior, *b*, posterior views. Original, from Rept. U. S. G. G. Surv. W. of 100th mer., G. W. Wheeler.

instead of four crescents, these teeth should possess four cones or tubercles perhaps more or less flattened. Such forms are already

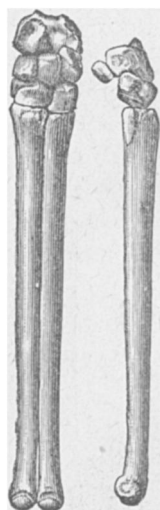


FIG. 3. — Carpus, metacarpus and end of cubitus of *Poebrotherium wilsoni* Leidy. Original.

known as ancestral to some other Ruminantia, as for instance the genus *Anthracotherium*, where the external cones are flattened on the outer side, or *Dichobune*, where the cones are not flattened at all. In both of these genera there are five tubercles to the superior molars, and the lateral (II, v) digits are present. We possess some fragments, however, of a lost genus from the age of the *Poebrotherium* (the White River Miocene, or Oligocene), which very probably represents the one which fills the interval. This has been named *Stibarus* (Cope), and it is only known from parts of lower jaws which contain premolar teeth. These have a great resemblance to the corresponding parts of an older genus of the same line, *Pantolestes*, from the Wasatch formation or Lower Eocene. It might be suspected that *Stibarus* is a member of the *Pantolestidæ* but for one fact. The superior molars of *Pantolestes* belong to the primitive type which has only three tubercles or cusps. No genus of ungulate mammals having this character is known to pass the bounds of the Eocene series of epochs in any country, and it is extremely improbable that *Stibarus* will prove to be an exception to this rule. I have very little doubt that the superior molars will be found to be quadritubercular, but it is impossible to be certain whether the tubercles are simple or crescentic. The resemblance of the premolars to those of *Pantolestes* leaves the probabilities in favor of their being simple. In this case *Stibarus* represents a family in the wide interval between the *Pantolestidæ* and the *Poebrotheriidæ*.

Messrs. Scott and Osborn have described a mammal, from the Bridger Eocene of Wyoming, as a probable member of the camel series, under the name of *Ithygrammodon cameloides*. It is only known from two premaxillary and a part of one maxillary bones. The former are slender and bear a complete set of incisor teeth, which are followed by a large canine. It is probable that this genus belongs in the camel series, but it cannot yet be positively affirmed.

The question of the origin of the Pantolestidæ is that of the origin of the suborder Artiodactyla. This I have believed would be found to have been from some yet undiscovered type or suborder of the order Amblypoda.¹ None of the known families of that order can have occupied this position, for although their general organization is appropriate, their superior and inferior molar teeth have been modified too much from the simple tritubercular type on which they are built. The ancestor of Pantolestes was an amblypod with the tubercles of its tritubercular superior molars entirely simple or conical. No such form has yet been discovered, but I have, in anticipation of such discovery, named the suborder the Hyodontæ.

Dr. E. Schlosser in an abstract of an unpublished memoir to



Fig. 4.

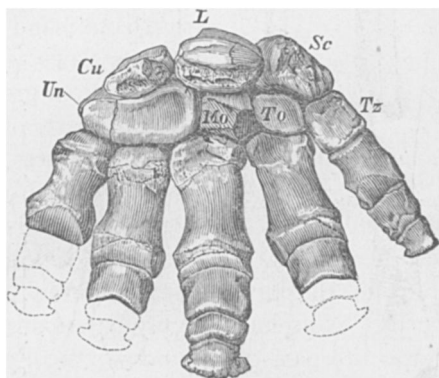


Fig. 5.

FIG. 4.—Left anterior foot of *Phenacodus primævus*, one-third natural size (original). FIG. 5.—Manus of *Coryphodon* (original). The cuneiform is imperfect. *Sc*, scaphoid; *L*, lunar; *Cu*, cuneiform; *Tz*, trapezium; *To*, trapezoides; *Mg*, magnum; *U*, unciform.

appear in the *Morphologisches Jahrbuch*,² takes the position that the Artiodactyla have been directly derived from the Taxeopoda and from the family of the Periptychidæ, thus leaving the Amblypoda out of their phylogeny. In this I cannot agree with him,³ and for the following reasons:

The evolution of the Diplarthrous, or alternate wrist-and-ankle-boned Ungulata (Fig. 6), from the Taxeopoda, or straight-rowed wrist-and-ankle-boned Ungulata (Fig. 4), has been by the rotation

¹ Proceedings Amer. Philosoph. Society, 1882, p. 447. Report U. S. Geol. Survey Terrs., III, 1885, p. 382.

² Zoologischer Anzeiger, 1886, No. 222.

³ On condition that the carpus of the Periptychidæ (which is unknown) is taxepodous, as I have supposed.

inwards of the second row on the first, in both the fore and hind feet. This rotation has resulted sooner or later in the loss of the internal digit (thumb and great toe) from both extremities. In the history of this sliding inwards of the second row, the outside element of the row has always preceded in time the inside element. The Amblypoda (Fig. 5) show this clearly. The unciform bone has extended inwards, so as to support the second bone of the first row (lunar) in part as well as the one which properly rests on it (cuneiform). But the magnum has not slipped inwards so

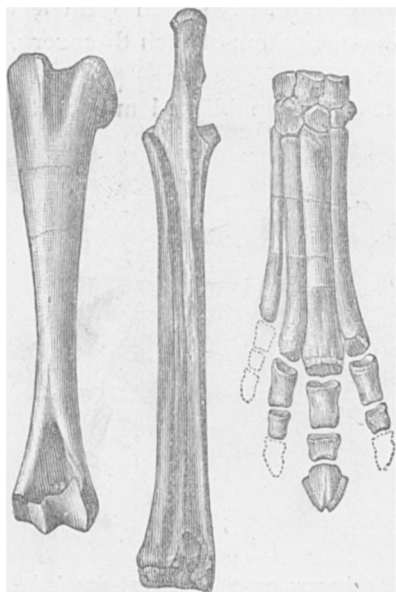


FIG. 6.—Fore-leg and foot of *Hyracoetherium venticolum* Cope, two-thirds nat. size; from Eocene beds of Wind river, Wyoming. Original, from Report U. S. Geol. Surv. Terrs., III.

as to support the scaphoid of the first row. That continues to be supported by its proper successors below, the trapezoides and the trapezium, the latter taking half the burthen. This structure (Fig. 5) is absolutely intermediate between that of the Taxeopoda (Fig. 4), and that of the Diplarthra (Fig. 6), and I imagine that all ungulates in passing from the taxeopodous to the diplarthrous stages traversed the amblypodous. The only other conceivable path would have been through a type in which the magnum had extended to below the scaphoid, while the unciform did not pass inwards beyond the limits of the cuneiform. No such type has

been found. On the other hand, I have shown that the Oreodontidæ¹ have pushed the transposition of the bones of the second carpal row to such an extreme that the magnum has gotten entirely under the scaphoid, while the unciform supports the lunar completely. Thus the alternating position with its useful mechanical consequence has been lost to this group, the effect produced being exactly that seen in the Amblypoda. This may have had something to do with the extinction of the Oreodontidæ.

¹ Proceedings Amer. Philos. Soc. 1884, pp. 504-9, and 1884, p. 23 (Palæontolog. Bull., No. 39).

The following suggestions as to the origin of the three peculiarities of the cameloid series, or Tylopoda as they have been called, may be made. The imperfection of the distal metapodial keels (Figs. 2, 3 and 7) is probably due to the early development of an elastic pad of connective tissue beneath the proximal phalanges. It is this pad which gives the foot of the camel its peculiar lateral expansion, and causes its step to be both elastic and silent. This structure has relieved the metapodials of the concussions to which the feet of other Ruminantia are subject, and I have advanced this fact as the cause of the peculiarity of the metapodials above mentioned.¹ The cause of the absence of superior incisor teeth is unknown, but has been supposed to be complementary to the presence of horns in the Ruminantia. None of the camel line have horns, and the presence of the single incisor on each side may be connected with this fact; but why two of the incisors on each side should have been lost under the circumstances, is not explained. Nor has any explanation been offered for the absence of the vertebrarterial foramina of the cervical vertebræ (Fig. 1).

There have been six species of the *Pantolestidæ* described, all belonging to the genus *Pantolestes*. The only ones of the six which are known from parts of the skeleton, are the *P. longicaudus* Cope, of the Bridger Eocene epoch, and the *P. brachystomus* of the Wasatch Eocene (Fig. 8). Neither of these species exceeded an existing musk-deer in size, and both had slender limbs. The tarsus of the *P. brachystomus* is known, and it is truly ruminant, though all the bones are distinct (Fig. 8). At the upper end the adjacent sides of the metatarsal bones are flattened and applied together, so that the later formation of a cannon bone by their fusion, must have been of easy accomplishment. The distal parts of these bones as seen in the *P. longicaudus* are not closely appressed, but are quite distinct from each other. The *P.*

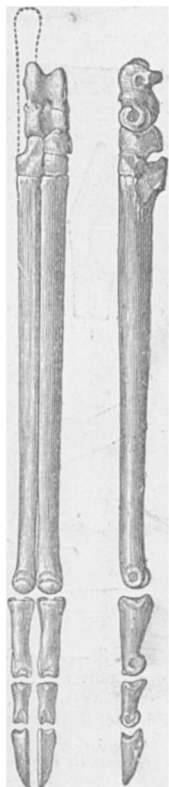


FIG. 7. — Hind foot of *Poebrotherium labiatum* from specimen represented in Fig. 1. Original, from White River Miocene of Colorado.

¹ AMERICAN NATURALIST.

etsagicus, also from the Wasatch Eocene of the Big Horn river, is represented by a portion of a robust lower jaw as large as that of a fox.

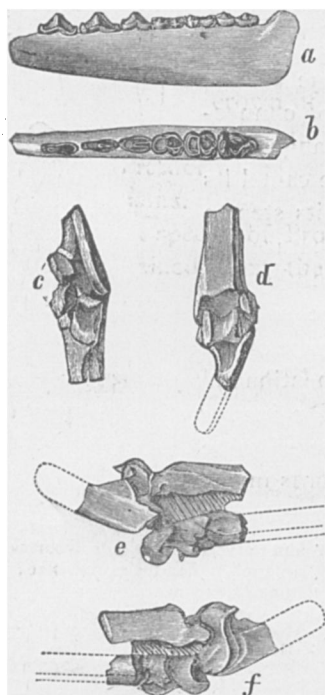


FIG. 8.—*Pantolestes brachystomus* Cope, nat. size, from Wasatch Eocene of Wyoming. Fig. *a*, superior molar teeth from below; *b*, mandible, left side; *c*, do. from above; *d*, tarsus with part of leg and metatarsus from before; *e*, from outside; *f*, from inside. Original, from Report U. S. Geol. Survey Terrs., Vol. III, F. V. Hayden.

But one species of *Stibarus* is known, and that from jaw fragments only in my museum and in that of Princeton College. These fragments appear to have belonged to an animal of the size of a pine weasel or martin, but the premolar teeth are very large for the size of the jaw and may indicate a larger animal. The anterior ones, ? first and second, have two roots each, and are quite elongate in the fore and aft direction. They are separated by a very narrow diastema from the tooth in front of them, ? the canine. The premolars are compressed and have a straight median cutting edge. This edge is thrown into two lobes between the anterior and posterior basal ones, the anterior only being the larger. The whole tooth resembles a rather low premolar tooth of a dog, and was evidently quite effective as a cutter of soft substances.

Of the Poebrotheriidae there are two genera. These differ as follows :

First premolar of upper jaw elongate and with two roots *Poebrotherium* Leidy.

First upper premolar short and with a simple conic root *Gomphotherium* Cope.

In *Poebrotherium* we have two species, a larger *P. labiatum* Cope, and a smaller *P. wilsoni* Leidy (Fig. 9). Both are animals of graceful and slender proportions, of about the size and build of the existing gazelles. Their heads were, however, of a more narrowed form towards the end of the muzzle. The remains of these animals have been found in the White River beds of Ne-

braska, Dakota, Wyoming and Colorado. They were evidently very abundant during Oligocene time.

The genus *Gomphotherium* embraces but one species, the *G.*

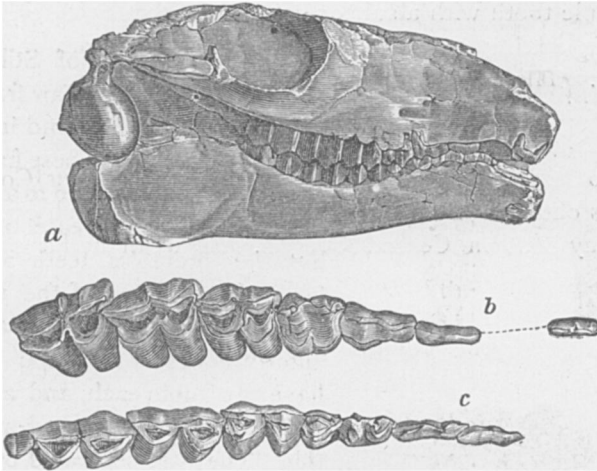


FIG. 9.—*Poebrotherium wilsoni* Leidy, from White River Miocene of Nebraska. Fig. *a*, skull, right side, one-half natural size; *b*, superior molar teeth, nat. size; *c*, inferior molars, nat. size. From Leidy, Ancient Fauna of Nebraska.

sternbergi Cope, which was found by Mr. C. H. Sternberg in the John Day Miocene beds of Central Oregon. Its size exceeds that of either of the *Poebrotheria*, equaling that of a llama.

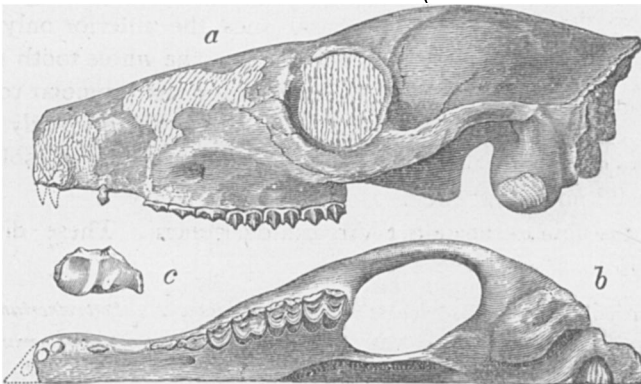


FIG. 10.—*Gomphotherium sternbergii* Cope, two-fifths nat. size, from the John Day Miocene of Oregon. Fig. *a*, left side; *b*, inferior side; *c*, distal end of radius. Original, from Report U. S. Geol. Survey, F. V. Hayden.

Its limbs were also slender, and in their general characters resemble those of the genus which preceded it. The second and fifth digits are represented on both feet by small scale-like bones

adherent to the sides of the two median metapodials. The inferior premolars in this genus are all much compressed, but differ much in form from those of *Stibarus*. The first upper premolar is a simple tooth with a subconical crown, totally different from the long cutting crown of the corresponding tooth in *Poebrotherium*. The next two premolars alone are compressed, though the third is rather wide posteriorly. The fourth is like that of other ruminants.

The oldest species of *Protolabis*, *P. transmontanus* Cope (Fig. 11), was obtained from the Ticholeptus beds, which overlie the John Day beds in Central Oregon. Its skull and a few bones

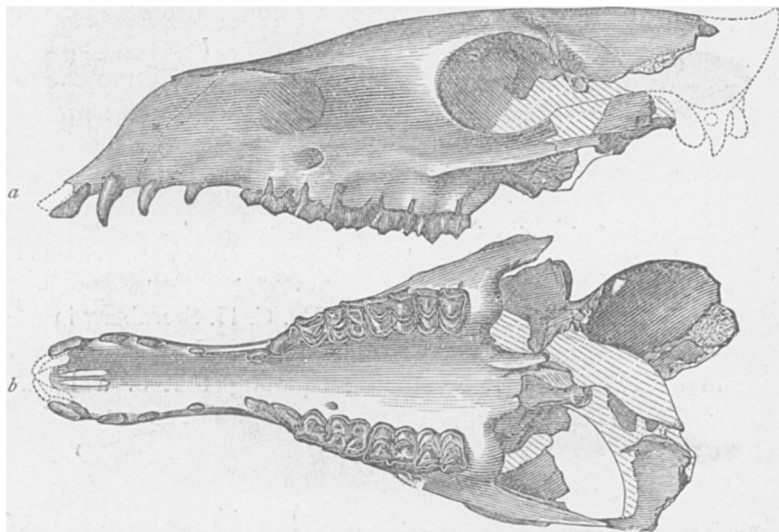


FIG. 11.—*Protolabis transmontanus* Cope, skull one-third nat. size, from Ticholeptus bed of Oregon. Fig. *a*, from left side; *b*, from below. Original.

only are known, but the former displays very complete dentition. Its size is about that of the Virginia deer. Its dimensions are in strict accord with the rate of increase of size to be observed in this series, and which it will be noticed, is maintained to the Pliocene epoch, when the greatest dimensions were attained. Two species of *Protolabis* appear in the succeeding or Loup Fork epoch which exceed the *P. transmontanus* in size. These are the *P. heterodontus* and the *P. prehensilis* Cope.

Accompanying the latter we have the species of *Procamelus* Leidy, the earliest members of the true Camelidæ. Its species vary in size from that of a sheep, as *P. gracilis* Leidy, to that of a deer, *P. occidentalis* Leidy, and to that of a camel, *P. robustus*

Leidy. The *P. occidentalis* (Fig. 12) appears to occur wherever the Loup Fork beds exist, from New Mexico north and east to Dakota. The *P. angustidens* Cope, intermediate in size between this form and the *P. robustus*, is not rare in Kansas and Colorado. Six or seven species of this genus have been named, one of them from teeth found near Richmond, Virginia. Species of the genus probably occur in beds of corresponding age in Florida.

Pliauchenia has been found as yet only in New Mexico, in two species not well preserved. It is not certain that any species of

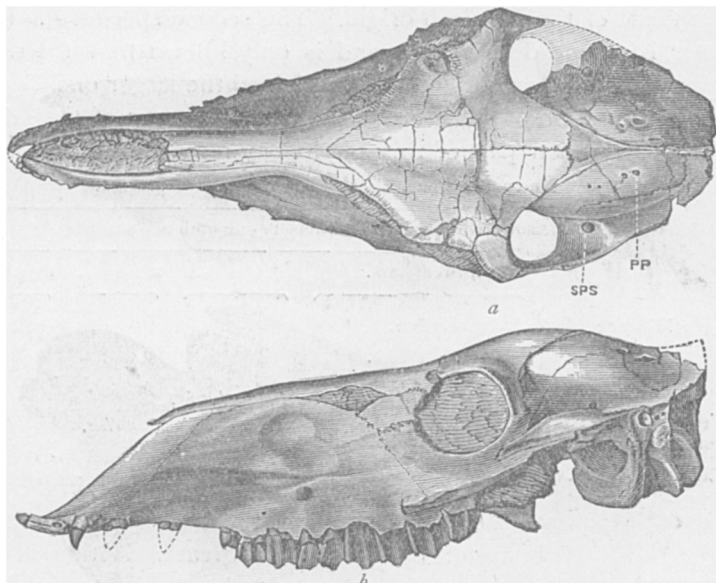


FIG. 12.—*Procamelus occidentalis* Leidy, one-third nat. size, from Loup Fork bed of New Mexico. Fig. *a*, skull from above; *b*, do. from left side. Original, from Report U. S. Expl. Surv. W. 100th mer., Vol. IV, G. M. Wheeler.

the genus *Auchenia* (llama) has been found fossil within the United States, though several have been described. Some or all of these belong to *Holomeniscus* Cope, which has only one premolar above, while *Auchenia* has two. A species about as large as a large llama has been found in the Oregon desert and named *H. vitakerianus* Cope. Another as large as the largest known camel is the *H. hesternus* Leidy. This fine species ranged from Oregon through California to the valley of Mexico, where it has been found by Professor Castillo of the School of Mines. A still larger species, perhaps of this genus, the *H. californicus* Leidy, must have exceeded in its dimensions either of the living camels. It is known from a few bones from California, and perhaps from Mexico.

The most specialized of all the genera of Camelidæ, *Eschatus* Cope, extended its range from Oregon to the valley of Mexico. I owe to the courtesy of my friend Dr. Mariano Barcena, formerly director of that department of the Museo Nacional of the City of Mexico, the opportunity of inspecting specimens of the jaws and teeth of this genus. It is represented by two species. The larger, *E. condens* Cope, was about as large as a camel or dromedary. It ranged from the valley of Mexico to Oregon; specimens found by Mr. Sternberg in the latter region not being distinguishable from those of the Mexican origin. The second species, *E. longirostris*, is a good deal smaller, and is only known from the same Equus beds of Oregon which have yielded the larger one.

The succession of structure in the leading genera of the selenodont or tylopod part of this phylogeny may be represented as follows :

	No cannon bone.	Cannon bone present.			
	Incisor teeth present.	Incisors one and two wanting.			
	4 premolars.	3 prem's. ¹	2 prem's.	1 prem'r.	
Lower Miocene	{ <i>Poebrotherium.</i>				
Upper Miocene	{ <i>Protolabis.</i> <i>Procamelus.</i>				
		{ <i>Pliauchenia.</i>			
Pliocene and recent			{ <i>Camelus.</i>		<i>Auchenia.</i>



FIG. 13.—Cast of brain of *Poebrotherium*, one-half nat. size. From Bruce, in Bulletin of E. M. Museum, Princeton, N. J.

This table shows that geological time has witnessed, in the history of the Camelidæ, the consolidation of the bones of the feet and a great reduction in the numbers of the incisor and premolar teeth. The embryonic history of these parts is as follows: In the foetal state all the Ruminantia (to which the camels belong) have the cannon bones divided as in *Poebrotherium*; they exhibit also incisor teeth, as in that genus and *Protolabis*. Very young recent camels have the additional premolar of *Pliauchenia*. They shed this tooth at an early period, but very rarely a camel is found in which the tooth persists. The anterior premolar of the normal *Camelus* is in like manner found in the young llama (*Auchenia*), but is shed long before the animal attains maturity. I may add that in some species of *Procamelus* caducous scales of enamel and dentine in shallow cavities represent the incisive dentition of *Protolabis*.

¹ In lower jaw.

In greater detail, the extinct American forms of this line are distributed as follows:

	Eocene.		Miocene.			Pliocene.	
	Wasatch.	Bridger.	White River.	John Day.	Ticholeptus.	Loup Fork.	Equus.
Pantolestes Cope	5	I					
Ithygrammodon S. O.		I					
? Stibarus Cope.....			I				
Poebrotherium Leidy.			2				
Gomphotherium Cope.				I			
Protolabis Cope.....					I	2	
Procamelus Leidy						6	
Pliauchenia Cope.....						2	
Holmeniscus Cope ...							3
Eschatus Cope.....							2

The total number of genera, nine; of species, twenty-six.

The development of the brain displays the same progress that has been shown by Lartet and Marsh to have taken place in other lines of Mammalia. The accompanying figures of the brain, show that while the *Procamelus occidentalis* is inferior to the camel in the size and development of the convolutions of the hemispheres, it is in advance of the *Poebrotherium wilsoni* in these respects (Figs. 13-14).

The development of the camels in North America presents a remarkable parallel to that of the horses. The ancestors of both lines appear together in the Wasatch or lowest Eocene, and the successive forms develop side by side in all the succeeding formations. Camels and horses are

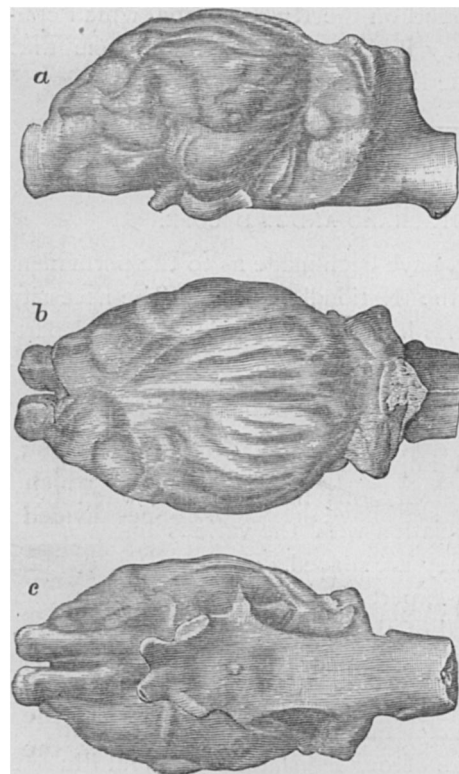


Fig. 14.—*Procamelus occidentalis*, cast of brain from skull represented in Fig. 12, one-half nat. size. Original, from Report U. S. G. G. Surv. W. of 100th mer., 1877, Vol. IV, G. M. Wheeler.

standard types in all our Tertiary formations; and they must be learned by

any one who wishes to distinguish readily the horizons one from the other. The horse-forms are more numerous in all the beds, in individuals as well as in species. Both lines died out in North America, and of the two, the camels only have certainly held their own in South America. The history of the succession of horses in Europe, although not as complete as that in America, extends over as wide a period of time. Not so with the camels. There is no evidence of the existence of the camel line in the old world prior to the late Miocene epoch; and so far as the existing evidence goes, the new world furnished the camel to the old.

Camelidæ only appear in South American palæontology in the genus *Auchenia*, in Pliocene time, in the Pampean beds. The best known species are *Auchenia weddellii* and *A. intermedia* of Gervais. It is curious that M. Ameghino, in his report on the fauna of the Miocene age found on the River Parana, which contains the ancestors of so many Pliocene genera, finds none that stand in that relation to these llamas.

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EDITORS' TABLE.

EDITORS: A. S. PACKARD AND E. D. COPE.

— Various suggestions have been made as to the permanent organization of science at the National Capital. The necessity for the employment of experts having been felt in various departments of the Government, commissions and offices for the conduct of research have grown up in them. The results have been greatly to the advantage of the Government and of the people, and have often represented important advances of science itself. The efficiency of these commissions has, however, often been impaired through their association with the various bureaus and departments under which they are placed. This comes from their necessary direction by non-experts and the quantity of routine work which may be required of them. There is also necessarily more or less overlapping of the similar offices in the different departments. Many of the commissions have been from time to time threatened with total extinction through the want of knowledge of their utility by some of our legislators. Several illustrations of this fact have recently occurred in Washington. The able superintendent of the Coast Survey has been removed, and his place taken by superior clerk of the Treasury Department.